Hydraulic redistribution in a Douglas-fir forest: lessons from system manipulations

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ABSTRACT

Hydraulic redistribution (HR) occurs in many ecosystems; however, key questions remain about its consequences at the ecosystem level. The objectives of the present study were to quantify seasonal variation in HR and its driving force, and to manipulate the soil–root system to elucidate physiological components controlling HR and utilization of redistributed water. In the upper soil layer of a young Douglas-fir forest, HR was negligible in early summer, but increased to 0.17 mm day^{-1} (20–60 cm layer) by late August when soil water potential was approximately −1 MPa. When maximum HR rates were observed, redistributed water replenished approximately 40% of the water depleted from the upper soil on a daily basis. Manipulations to the soil or to the soil/plant water potential driving force altered the rate of observed HR indicating that the rate of HR is controlled by a complex interplay between competing soil and plant water potential gradients and pathway resistances. Separating roots from the transpiring tree resulted in increased HR, and sap flow measurements on connected and disconnected roots showed reversal of water flow, a prerequisite for HR. Irrigating a small plot with deuterated water demonstrated that redistributed water was taken up by small understorey plants as far as 5 m from the watering source, and potentially further, but the utilization pattern was patchy. HR in the upper soil layers near the watering plot was twice that of the control HR. This increase in HR also increased the amount of water utilized by plants from the upper soil. These results indicate that the seasonal timing and magnitude of HR was strongly governed by the development of water potential differences within the soil, and the competing demand for water by the above ground portion of the tree.

Key-words: *Pseudotsuga menziesii*; deuterium labelling; hydraulic lift; seasonal variation; soil water utilization; soil water potential; trenching, water transport.

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INTRODUCTION

The passive movement of water via roots from wetter to dryer portions of the soil is known as hydraulic lift (Caldwell & Richards 1989; Caldwell, Dawson & Richards 1998), or more recently as hydraulic redistribution (Burgess *et al.* 1998), because water has been found to flow passively through roots both laterally (Brooks *et al.* 2002; Smart *et al.* 2005) and downward within the soil (Schulze *et al.* 1998; Smith *et al.* 1999; Burgess *et al.* 2000b; Ryel *et al.* 2002; Hultine *et al.* 2003a) along water potential gradients. The number of studies documenting hydraulic redistribution (HR) indicates that the process is common in plants that have an appropriate distribution of roots in soils that develop significant water potential gradients (Caldwell *et al.* 1998; Jackson, Sperry & Dawson 2000). HR has been found in all but a few species that met these requirements (Hultine *et al.* 2003b; Espeleta, West & Donovan 2004), so the capacity to hydraulically redistribute water appears to be the rule rather than the exception. Hydraulic redistribution has even been documented for CAM plants which transpire at night, so redistribution occurs during the daylight hours (Yoder & Nowak 1999). Most recently, hydraulically redistributed water has been found to be transferred to mycorrhizal symbionts (Querejeta, Egerton-Warburton & Allen 2003). The process has been documented to be important not only for recharge of the upper soil, but also for recharging deeper soils after precipitation events (Schulze *et al.* 1998; Burgess *et al.* 2000b; Ryel *et al.* 2002; Moreira *et al.* 2003). Uptake of hydraulically redistributed water by understorey plants has also been reported in some ecosystems through the use of deuterium tracers in the water (Caldwell *et al.* 1998; Brooks *et al.* 2002; Moreira *et al.* 2003).

In spite of the advances in documenting the occurrence of HR in numerous ecosystems, key questions remain about the amount of water that is hydraulically moved within an ecosystem, the underlying factors that control redistribution and its importance to plant function. Most studies have relied on daily fluctuations of soil water potential (Ψ_{soil}) to document HR (Dawson 1993a; Caldwell *et al.* 1998; Millikin Ishikawa & Bledsoe 2000; Ludwig *et al.*

2003; Espeleta *et al.* 2004). However, using changes in Ψ_{soil} to quantify the amount of water that is hydraulically redistributed requires accurate site-specific soil moisture release curves, which can change dramatically with depth because of vertical changes in soil texture and bulk density (Emerman & Dawson 1996; Warren *et al.* 2005). Nevertheless, a few studies have attempted to quantify the amounts of water hydraulically redistributed by plants. One of the first studies to do so was that of Emerman & Dawson (1996) who calculated soil moisture release curves for each psychrometer position. They found that an individual sugar maple tree was capable of lifting up to 100 L per day; however, they did not calculate the volume on a ground area basis such as in mm d^{-1}. For studies in which the dynamics of soil moisture content (θ) has been measured along with Ψ_{soil}, the amount of water actually moved appears to be relatively small, less than 1 mm of water per metre depth of soil per day, and mostly less than 0.5 mm m^{-1} d^{-1} (Song *et al.* 2000; Brooks *et al.* 2002; Meinzer *et al.* 2004). Meinzer *et al.* (2004) measured an average maximum of 0.35 mm m^{-1} d^{-1} across six sites differing in the abundance and size of woody vegetation, soil type and climate. However, this small amount of water is highly significant when considering the amount of water being utilized by the plants each day from the soil layer where HR is occurring. Brooks *et al.* (2002) found that HR can replenish 28–35% of the soil water removed each day by plants from the upper soil layers. This amount of HR was enough to delay drying of the upper soil by an additional 16–31 d before reaching the seasonal minimum θ. Meinzer *et al.* (2004) noted that as Ψ_{soil} declined, soil water use also declined but HR did not, resulting in HR replenishing up to approximately 80% of the water used on a daily basis from surface soils at low water potentials (–1.4 MPa). In certain forests, this replenishment was enough to keep Ψ_{soil} from reaching critically low values (Jackson *et al.* 2000). Domec *et al.* (2004) found that this delay in soil drying by HR was enough to decrease seasonal root embolism in the upper soil since Ψ_{soil} remained above the cavitation threshold for small roots for longer periods. Ryel *et al.* (2002) estimated in a model that HR can increase transpiration by 3.5% over a 100-day period and as much as 20% on some days. Thus, although the amount of water hydraulically redistributed is small, HR appears to play an important role in maintaining hydraulic function and transpiration over dry periods.

However, important questions remain about seasonal variability and the physiological variables governing HR. Brooks *et al.* (2002) monitored and quantified HR for a few weeks, but not over an entire season. Meinzer *et al.* (2004) found that HR began once Ψ_{soil} fell below a –0.4 MPa threshold, however, the determinants of the threshold for onset of HR are not fully understood. The objective in the present study was to quantify the magnitude of seasonal variation in hydraulic redistribution and its driving force and to manipulate the soil-root system to tease apart important components of control over HR, and its influence over water utilization. We monitored soil water utilization and HR in a young Douglas-fir stand that experiences a significant summer dry period typical for the Pacific Northwest. In addition, we manipulated the soil–root system through irrigation with labelled water, soil trenching, and tree removal experiments to understand the interplay between water potential differences in the soil, and competition from the above ground portion of the tree on the rate and magnitude of HR.

MATERIALS AND METHODS

The study site was located in an approximately 25-year-old stand of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) at about 558 m elevation in the Gifford Pinchot National Forest in southern Washington (45°49'07.89" N, 121°59'38.95" W) adjacent to the Wind River Canopy Crane Research Facility (WRCCRF, http://depts.washington.edu/wrccrf/). The dominant Douglas-fir trees were approximately 17 m tall and 20 cm diameter at breast height, forming a dense closed canopy with an understorey dominated by Oregon grape (*Berberis nervosa* Pursh), small hemlocks (*Tsuga heterophylla*), huckleberry (*Vaccinium* spp.) and salal (*Gaultheria shallon* Pursh). Stand density and basal area were estimated to be 3057 trees ha^{-1} and 46.9 m^2 ha^{-1}, respectively (Phillips *et al.* 2002). The soil was a deep, well-drained, medium-textured sandy loam classified as a medial mesic, Entic Vitrand (Klopatek 2002) consisting of 56% sand, 34% silt, and 10% clay in the upper 40 cm (Warren *et al.* 2005). Average annual precipitation and temperature at the open meteorological station at WRCCRF is 2223 mm year^{-1} and 8.7 °C, respectively. However, precipitation is highly seasonal with most precipitation falling between October and May, resulting in a significant summer dry period in this region (Shaw *et al.* 2004). Precipitation data presented in this paper are from the open meteorological station at WRCCRF, which is located approximately 3.5 km east of the study location. Coarse roots in this stand have a wide variety of morphology including lateral, sinker, tap and knee roots (laterals that turn down), and a profuse branching nature (Goebel 2002).

To accomplish the study objectives, three experimental plots were set up within the stand. Topography within the plots was relatively flat. A base-line or control plot was established where soil volumetric moisture content (θ) and water potential (Ψ_{soil}) were monitored through the dry period from June to September 2002 to quantify natural rates of soil water depletion and HR. An irrigation plot was established over 100 m away from the control plot, where deuterated water was used to detect water being moved laterally by HR and uptake by neighbouring plants. The irrigation plot was located in a flat region of the stand where the slope was less than 1% in 20 m radius from the point of irrigation. Finally, a 1 m deep trench was dug around a 2 m × 2 m plot with no Douglas-fir trees to decrease HR, and this plot was located 15 m away from the control area in a canopy gap. Details on measurements and methods for each plot follow below.

Soil water status

At all three plots, soil volumetric moisture content was measured using a multisensor frequency domain capacitance technique (Paltineanu & Starr 1997; Starr & Paltineanu 1998). A probe consists of multiple annular capacitance sensors (Sentek PTY LTD, Adelaide, Australia) separated by 10 cm or more, mounted to a plastic shaft and placed in weatherproof PVC access tubes installed to a desired depth. These probes are relatively insensitive to fluctuations in soil temperature (3.5×10^{-4} change in vol. water content $°C^{-1}$ between 10 and 30 °C; (Paltineanu & Starr 1997), and the maximum diurnal variation in soil temperature at 20 cm in this stand was 1.1 °C. The control plot had three probes installed to a depth of 2 m with eight independent sensors per probe. The trench plot had one probe with eight sensors, and the irrigation plot had two probes with two sensors each. In total, 36 independent sensors of soil moisture were continuously monitoring soil moisture for this study. Sensors on each probe were located at 20, 30, 40, 50, 60, 100, 150 and 200 cm depth in the control and trench plot, and at 20 and 30 cm depth in the irrigation plot. Each sensor was monitored every 10 min and the measurements were stored in a data logger (model RT6; Sentek, Adelaide, Australia). Sensors were calibrated in the field for the air and water frequency reading endpoints for determination of the normalized frequency. Normalized frequency readings were converted to volumetric soil moisture content using a site-specific calibration equation (Warren *et al.* 2005), which is necessary to obtain absolute values of θ. We found that the default factory calibration equation under-estimated θ by over 15% for the specific sandy loam soils of the Pacific Northwest.

Soil water storage, measured in millimetres of water within a specified layer of soil (e.g. 20–60 cm), was calculated by summing the volumetric water content for each 10 cm sensor within that layer. Each sensor reports θ data as (m^3 water/m^3 soil) $\times 100$ which is equivalent to millimetres water per 10 cm soil depth which the sensor monitors, so summing each sensor results in millimetres of water within the layer. When there was a gap between sensors such as between 60 and 100 cm, θ in the intervening layer was interpolated as an average of the sensors above and below the gap. Total daily water use was calculated as the difference between the maximum and minimum soil water storage measured within a daily time period. HR was defined as the nightly increase in θ, and was calculated as the difference between the minimum θ of one day and the maximum θ of the next day. From previous work (Brooks *et al.* 2002), we found that HR was restricted to the upper 60 cm of soil, so HR was calculated for the 20–60 cm soil layer in mm d^{-1}. The HR calculation could be performed in two ways giving either total HR within 20–60 cm, or net HR for the layer. Net HR represents the amount of water imported into the 20–60 cm layer over night, whereas total HR also includes movement of water within the layer from one 10 cm sensor to another. For total HR, HR was calculated for each individual sensor (20, 30, 40, 50 and 60 cm)

and then summed for all the sensors. For net HR, soil water storage was calculated first for 20–60 cm using the 10 min data for all the sensors within that layer, and then a single net HR was calculated for that layer using soil water storage data.

Soil water potential was measured using soil psychrometers (PST-55, Wescor Inc. Logan, UT, USA) placed at 20, 30, 40, 50, 60 and 100 cm depth in the control plot at four locations and at 20, 40 and 60 cm depth in the trench plot at one location for a total of 27 soil psychrometers. The psychrometers were individually calibrated in the laboratory prior to placement in the field using salt solutions of known osmolality and their calibration factors were determined following the procedures of Brown & Bartos (1982). For the control plot, the psychrometers were installed in June and measured throughout the summer. For the trench plot, the psychrometers were installed in August but only measured in September due to datalogger limitations. Ψ_{soil} was measured every 30 min using a 30 s cooling time for the Peltier effect and data were recorded on a datalogger (CR-7; Campbell Scientific, Logan, UT, USA). Predawn leaf water potential (Ψ_{leaf}) was measured monthly using a portable pressure chamber (PMS Instruments, Corvallis, OR, USA). At each sampling date, five foliage samples were collected from the tops of trees accessed by a tower. Measurements were corrected for gravity so that leaf values are comparable to Ψ_{soil}.

Deuterated water experiments

To monitor the potential for water to migrate laterally via hydraulic redistribution and be taken up by surrounding plants (e.g. Brooks *et al.* 2002), a 1 m^2 watering plot was located at the edges of the crowns of four target trees, with the idea that these four trees would directly take up the water and hydraulically redistribute it to the soil and shallowly rooted plants located at distances from 1 to 5 m from the watering plot. About 2100 L of water enriched with deuterium to +7000‰ were applied with a watering wand at a slow trickle to the plot for three weeks (14–30 August 2002). A circular plastic barrier was placed on the soil surface where the water was applied to prevent runoff and ensure that all the water infiltrated into the soil within the 1 m^2 area. Samples for δD and $\delta^{18}O$ analysis in plant and soil water were collected in glass vials with polyseal cone inserts in the cap and sealed to prevent evaporation. Samples were collected prior to deuterated water application, and approximately weekly for 5 weeks after the irrigation began. Samples from the target Douglas-fir trees were collected using a 12-mm diameter increment borer (Haglöf Inc., Långsele, Sweden), whereas suberized branch or stem tissue was clipped from other plants. Soil samples were collected at 10 cm depth near the base of the target trees, on the side nearest the watering plot, but over 1 m from the edge of the watering plot, and on the far-side of the target trees.

Water was extracted from the plant and soil samples using cryogenic vacuum distillation (Ehleringer & Osmond

1989; Dawson 1993b; Ehleringer, Roden & Dawson 2000). Water samples were analysed for δD and $\delta^{18}O$ on an isotope ratio mass spectrometer (Delta plus; Finnigan, Bremen Germany) interfaced with a high-temperature conversion/ elemental analyser (TC/EA; ThermoQuest Finnigan, Bremen, Germany) located at the Integrated Stable Isotope Research Facility at the Western Ecology Division of the EPA, Corvallis Oregon. All δD and $\delta^{18}O$ values are expressed relative to Vienna-standard mean ocean water (V-SMOW) in ‰

$$\delta D \text{ or } \delta^{18}O = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) 1000$$

where R is the ratio of deuterium to hydrogen atoms or ^{18}O to ^{16}O atoms of the sample and the standard V_SMOW. Measurement precision was 2‰ for δD and 0.3‰ for $\delta^{18}O$.

Measurements of $\delta^{18}O$ were used so that δD values enriched from the tracer could be distinguished from δD values enriched from evaporation. Both δD and $\delta^{18}O$ of water become enriched through evaporation, whereas only δD increases with additions of D_2O. The natural abundance variation in δD and $\delta^{18}O$ of water from plant and soil samples at the site are related linearly along a local evaporation line $(\delta D = -43.6 + 4.2\delta^{18}O, R^2_{adj} = 0.89, N = 94)$. Natural abundance δD values varied from −58.7 to −107 with a mean of −85.7‰; however, once the variation in $\delta^{18}O$ was accounted for, natural abundance δD values only deviated by a maximum of 8‰ above the line. Samples were determined to be enriched if they fell above that 8‰ range around this evaporation line. As a result, water containing 0.1% of the tracer water could be reliably distinguished from natural abundance levels.

Trenching experiment

A 2 m × 2 m trench plot was established in a gap within the stand on 19 July 2002 in order to test the hypothesis that trenching would reduce HR. The trench was 1 m deep and at least 30 cm wide and surrounded the plot. Roots within the trench were severed and removed, and then the trench was lined with landscape fabric to prevent root in-growth so that the entire soil face of the 2 m × 2 m plot was covered down to 1 m depth. The trench was refilled with the original soil and compacted so that soil water did not evaporate directly from the sides of the trench during the experiment. Care was taken so that the vegetation and soil within the plot were minimally disturbed. The soil moisture probe and soil psychrometers were located in the centre of the plot (see above for sampling depths). Due to unavailability of a suitable datalogger, water potential was only monitored in the trench plot in the period 3–8 September 2002, but θ was measured continuously from 19 July.

Root sap flow, tree and root cutting experiment

In order to detect the relative influence of transpiration and hydraulic redistribution on root sap flow, we selected a tree for root and stem cutting experiments. The tree was selected for accessibility and being located well away from our control plot so as not to influence the results there. Ten lateral-appearing roots were excavated around one-half of the base of the tree for installing root sap flow sensors. The roots ranged in diameter from 15 to 65 mm with an average of 30 mm (± 15 mm SD). After an initial period of monitoring for evidence of HR, a forked root where each fork was being measured was detached from the tree and monitored for a period of time. Finally, the tree itself was felled and root sap flux monitored.

Root sap flow was measured with the thermal dissipation technique (Granier 1987) modified to permit the direction of flow to be detected (Brooks *et al.* 2002; Brooks & Coulombe unpubl. data). In its original form, this technique indicates the magnitude of flux only and is insensitive to the direction of flow, and is thus not suitable for monitoring reversal of flow in roots associated with hydraulic redistribution (Burgess, Adams & Bleby 2000a). However, we have added a directional probe which allows the thermal dissipation method to be highly sensitive for detecting reversal of flow. For each root, a flux and a directional probe was installed. For the flux magnitude probe, a cylindrical heated temperature sensor, 10 mm in length was inserted into the xylem in the centre of the exposed root. Two unheated reference temperature sensors (10 mm in length) were placed axially 100 mm up- and downstream from the heater sensor and wired to measure the temperature differences between the heated and unheated sensors. For the directional probe, two thermocouples were inserted 8 mm axially to a depth of 7.5 mm up- and downstream from the heater probe. The movement of the heated water raised the temperature of the downstream thermocouple relative to that of the upstream thermocouple, providing a highly accurate and sensitive gauge to direction of flow (Brooks & Coulombe unpubl. data). The temperature of the reference probe that was determined to be upstream of the direction of flow was used to calculate sap flux density $(g\ m^{-2}\ s^{-1}$, Granier 1987). Sap flow moving toward the tree base was indicated as positive, whereas sap flow moving away from the tree base was indicated as negative. As the thermal dissipation technique requires, we assumed zero flow when the temperature differential of the flux magnitude probe reached its daily maximum. The directional probe temperature differential provided additional information that was very useful for interpreting the flux magnitude data and allowed us to determine when reverse flow was occurring. At the time when the flux probe signal reached its daily maximum (zero flow), the directional probe value was very close to zero, and we used that value to differentiate between positive and negative flow in the root. When a root is showing no reversal of flow, the flux probe reaches its maximum differential at the same time as the directional probe reaches its zero value, then as sap flux increases again, the directional probe differential increases as the flux probe differential decreases. When reverse flow is occurring, the directional probe value will drop below its zero value well before the flux probe reaches its maximum value, and then the directional probe value increases to its

zero value when the flux probe reaches its maximum value. When reversal of flow is high, the flux probe will have two peaks during the night, with the second peak always being of greater value than the first, but the differential probe will drop below its zero value after the first peak, and return to the zero value with the second peak.

RESULTS

The 2002 seasonal precipitation pattern was typical for this region in which 95% of the precipitation (2296 mm) occurs between October and May, with the remaining five percent (128 mm) falling during the summer months of June–September. The summer of 2002 had a prolonged dry period during which only 7 mm of rain fell between 1 July and 15 September (Fig. 1a). Ψ_{soil} in the upper metre was essentially zero until late July when it started decreasing above 1 m depth (Fig. 1b). Predawn Ψ_{leaf} (approximately –0.5 MPa) was relatively stable as Ψ_{soil} declined, resulting in predawn Ψ_{leaf} being lower than Ψ_{soil} until around mid August. On 10 September, Ψ_{soil} reached a minimum of –1.3 MPa at 20 cm depth, and –1.0 MPa at 60 cm depth, whereas at 1 m Ψ_{soil} was substantially higher at –0.3 MPa. Following a 15-mm rain event on 16 September, Ψ_{soil} increased at all depths above 1 m, but predawn Ψ_{leaf} was still low (–0.75 MPa) on 23 September.

Soil volumetric water content was at its maximum for the summer at the end of June following a 46 mm rain event (Fig. 1c). Water storage in the upper 2 m of soil was 695 mm after this rain event, with a maximum θ of 41.5% at 2 m depth, declining toward the surface to 26.1% at 20 cm. Water content slowly declined through the season until a 15 mm precipitation event on 16 September. The decline was initially most rapid in the upper 60 cm during the early summer, but the rate of decline decreased through the summer. In contrast, water content in deeper layers was relatively stable in the early season, but declined slightly in the late summer. By the end of the summer, soil water storage in the upper 2 m had declined to 549 mm. Thus, 146 mm of water had either drained or been utilized by the forest. At 20 cm, θ had decreased to 11.3%, a loss of 14%, whereas at 2 m, θ was at 38.7%, having decreased by less than 3%. The stability of the deepest layers relative to the shallower depths indicate that soil drainage was probably negligible, and most losses were through transpiration (evaporation would be negligible at 20 cm depth).

The amount of water utilized in the upper 2 m of soil reached a maximum of 2.75 mm d^{-1} with an average of 1.95 mm d^{-1} through the summer (Fig. 1d). These rates are higher than but consistent with a mean rate of 1.4 mm d^{-1} reported by Chen *et al.* (2004) for this stand in 1999. Peak rates of soil water depletion (Avg. 2.5 mm d^{-1}) were observed through July when precipitation had stopped but Ψ_{soil} was near its maximum. During this time, the upper 50 cm of soil (20–60 cm) was contributing a similar amount as the lower 140 cm (60–200 cm) (1.2 versus 1.4 mm d^{-1}, respectively). As Ψ_{soil} began to decline in the upper soil, daily water depletion began to decline in the upper layer,
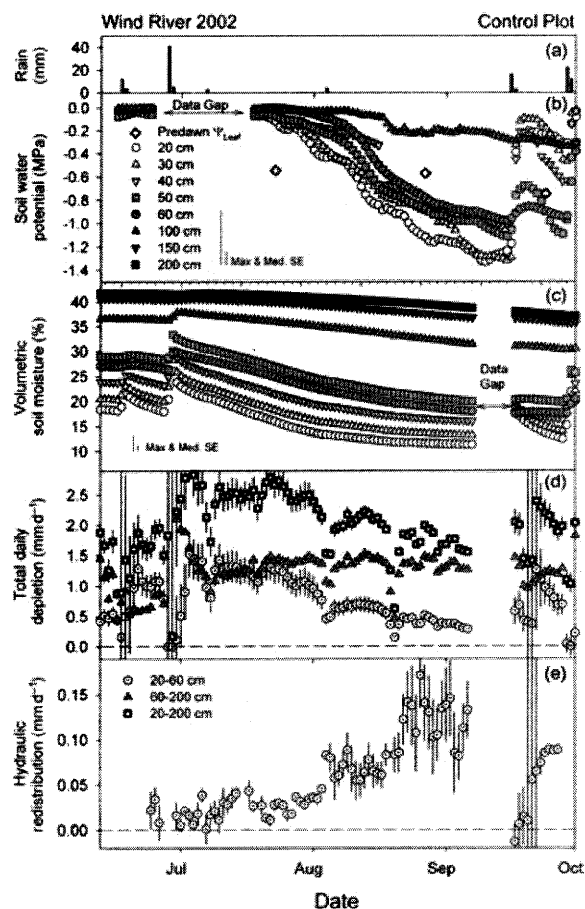

Figure 1. Seasonal patterns in (a) precipitation, (b) predawn leaf water potential (Ψ_{leaf}) and soil water potential, (c) volumetric soil moisture, (d) total daily water depletion, and (e) hydraulic redistribution (HR) for the control plot. For soil moisture and soil water potential, each depth value is the average of three or four sensors. Predawn leaf water potentials are an average of five readings and have been corrected for gravity to ground level so they are comparable to soil water potentials. See method for calculations of daily depletion and HR. HR is total lift within in the layer and is only shown for the 20–60 cm layer. Standard errors (SE) are based on variation in the daily values from the three or four probe locations. For visual reason, only the maximum and median SE values are reported for (b) and (c).

whereas in the lower layer, daily water depletion remained nearly constant if not slightly increasing. Thus depletion in the entire layer (20–200 cm) also declined. By early September, daily water depletion had declined to 1.5 mm d^{-1}, to which the upper layer was only contributing about 0.4 mm d^{-1}.

Early in the season, the amount of water redistributed in the upper 50 cm was negligible (< 0.05 mm d^{-1} to the upper 50 cm, Fig. 1e). However, when the amount of water utilized daily from the upper soil layer began to decline (late July–early August), the total amount of water hydraulically redistributed in this area began to increase steadily, reaching a maximum of 0.17 mm d^{-1} in early September. HR also

began to increase after Ψ_{soil} fell below predawn Ψ_{leaf}. At the end of the dry period, HR accounted for approximately 40% of the water utilized daily from the 20–60 cm soil layer.

The increase in HR through the season was related to the decrease in Ψ_{soil} within the upper layers (Fig. 2), which was roughly equivalent to the Ψ_{soil} gradient since soils at 1 m did not get below −0.2 MPa for this time period, and deeper soils were probably near zero. In the early season, total HR between 20 and 60 cm increased linearly with a decrease in water potential, but net water movement to the layer through redistribution was negligible, indicating that water was being hydraulically redistributed along water potential differences within the layer, and not coming from below 60 cm depth. However, when the Ψ_{soil} of the upper layer reached an average of −0.7 MPa, net redistribution to the layer increased rapidly as Ψ_{soil} continued to decline. When the average Ψ_{soil} was around −1 MPa, water was still being redistributed within the 20–60 cm layer, but at least one-half to two-thirds of the water was coming from below 60 cm.

Following trenching, HR was several fold higher than control rates because trenching separated large roots in the plot from neighbouring transpiring trees (Fig. 3). HR rose to 1.3 mm d⁻¹ in 20–60 cm layer following trenching, over 10 times that of naturally occurring HR measured in this stand, and in all other stands we have measured (Brooks *et al.* 2002; Domec *et al.* 2004; Meinzer *et al.* 2004; Warren *et al.* 2005, Warren, Brooks, Meinzer, Domec & Coulombe unpubl. data) Water storage within the 20–60 cm layer also increased from 116 to 124 mm over an 18 d period, another unprecedented observation for periods without precipitation. Meanwhile, water storage in the control plot decreased from 115 to 94 mm. After HR peaked, the amount of HR in the trench plot decreased over the next 2 weeks until it was similar to or slightly more than that at the control site. Thereafter, soil water storage remained relatively constant in the trench plot, but continued to decrease in the control plot. Ψ_{soil} was not measured in the

Figure 3. A comparison of hydraulic redistribution and soil water storage in the 20–60 cm layer after trenching a 2 m × 2 m plot to 1 m depth. The bars are the standard deviation of hydraulic redistribution between the three control plot probes.

trench plot until the beginning of September, when values were found to be around zero throughout the 5 d measurement period, even though a dense mat of Salal covered the trench plot (Table 1). Ψ_{soil} in the control plot during that time was significantly less than zero for the 20 and 40 cm layers. Soil moisture contents at the 40 and 60 cm depths were also significantly less than those in the trench plot.

Of the 10 major lateral roots where root sap flow was monitored, only three showed significant reverse flow over the entire monitoring period. In mid-August, only one
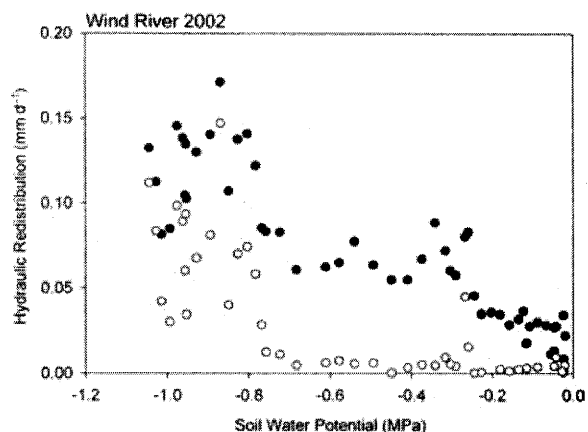

Figure 2. Rates of net (open symbols) and total (closed symbols) hydraulic redistribution (20–60 cm soil layer) as a function of the average soil water potential (20–60 cm) in the control plot.
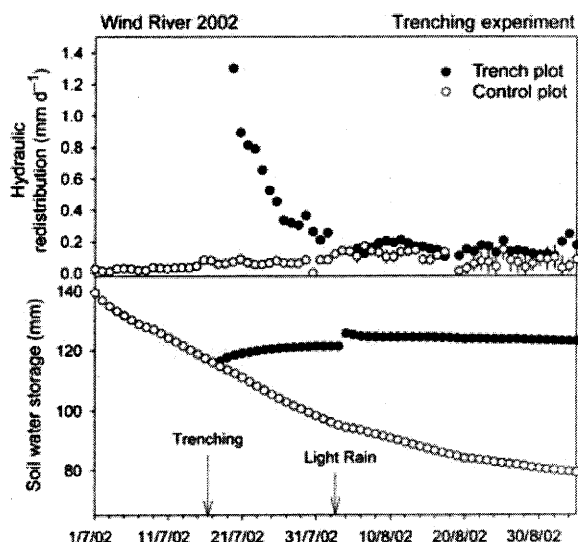
Table 1. Comparison between control and trench sensors for water potential, soil temperature, and soil moisture

	Depth (cm)	Control	Trench
Water potential (MPa)			
	20	−1.21 ± 0.18*	−0.01
	40	−0.91 ± 0.24*	−0.02
	60	−1.04 ± 0.40	−0.01
Soil temperature (°C)			
	20	11.8 ± 0.23	11.2
	40	11.8 ± 0.22	11.1
	60	11.3 ± 0.17	10.8
Soil moisture (%)			
	20	11.3 ± 1.2	15.7
	40	16.1 ± 2.5*	29.6
	60	18.1 ± 0.7*	24.0

The control sensors were replicated three to four times at each depth, whereas only one sensor at each depth was placed in the trench plot. Values are means from 3–8 September 2002. Standard errors between sensors were calculated for control sensors, comparing average values over the time interval. *Indicates that the control sensors are significantly different ($\alpha = 0.05$) from the trench value (*t*-test).
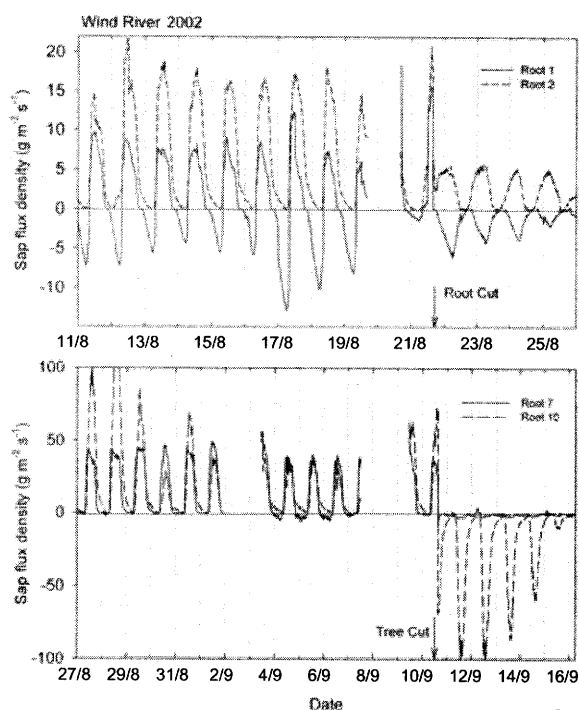
Figure 4. Time courses of sap flow in roots of a codominant Douglas-fir tree. A positive value means flow was towards the base of the tree, whereas a negative value indicates reverse flow away from the base of the tree. The vertical dotted lines indicate midnight. The arrows indicate the time that the manipulations occurred. Roots 1 (20 mm diameter) and 2 (15 mm diameter) were connected at a junction 10 cm from the trunk base, where root 1 was the upper root and root 2 was lower. Root 7 and 10 were 20 and 65 mm in diameter, respectively.

root was showing significant reversal of flow (Fig. 4). Roots 1 and 2 were a pair of roots from a lateral fork located about 10 cm from the base of the tree. In the root with reversal of flow (root 1), the daily transport up the tree was almost equivalent to the nightly transport back out to the soil. In contrast, flow continued towards the tree most of the night in the paired root not showing reversal of flow (root 2), and its daily rate was about twice that of the other root. On 21 August the root fork was severed from the tree, but the two roots remained in contact with each other. At this point, root 1 showed only reverse flow, and root 2 continued to show positive flow approximately equal and opposite in magnitude to root 1, indicating that root 2 provided the source of water for the

reversal of flow observed in root 1. However, the magnitude of flow did not increase.

In early September, root 7 also began to show reversal of flow at a similar magnitude to that of root 1 earlier (~5 g m^{-2} s^{-1}). However, the scale in second part of Fig. 4 does not clearly illustrate this, since root 7 had a much greater diurnal amplitude of fluctuation in flow than root 1. On 10 September the tree was felled, and flow ceased in most of the roots in which it was being measured (i.e. root 7). However, in the largest root (root 10) flow began to reverse with a magnitude equal to its greatest diurnal magnitude before felling. Since none of the other monitored roots showed either significant positive or negative flow, other unmonitored roots must have provided the source of water for this root. The diurnal behaviour of both sets of roots after severing their connection with the transpiring foliage is puzzling, but real, and not an artefact. The only plausible explanation is that a diurnally fluctuating water potential gradient was still present possibly through root grafting.

In the deuterated watering experiment to detect lateral movement of hydraulically redistributed water, the four target Douglas-fir trees picked up significant amounts of the label (Table 2). Deuterium values varied between 3450 and 1000‰ in xylem water taken from the trees, indicating that as much as 50% of it was obtained from the labelled water, but on average the proportion of labelled water constituted approximately 25% of the water in the xylem sap. These high levels reflect direct uptake of the deuterated water and were sufficiently high for the labelled water movement into the soil and surrounding plants to be tracked over a 5-week period (Fig. 5).

At the first sampling period 7 d after deuterated water was added to the system (20 August 2002), label was detected in soil samples (10 cm depth) collected nearest to but over 1 m from the watering plot at the base of the target trees, and one in Oregon-grape (Fig. 5). The amount of label found in the labelled samples was less than 1% from the deuterated source water (Fig. 6). However, given the dilution of the source water within the xylem of the target tree and then again from the soil water and from the xylem water of the plant that took up the water, these low values of label are realistic for redistributed water. At each sampling time, deuterated label was found further from the source, in more plant and soil samples collected, and at higher concentrations. After 21 d, deuterated water was found in a small understorey hemlock 4.5 m from the water source, and was detected in soils around most target trees

Table 2. The maximum and average amount of label found in the four target Douglas-fir trees over the 5 week sampling period

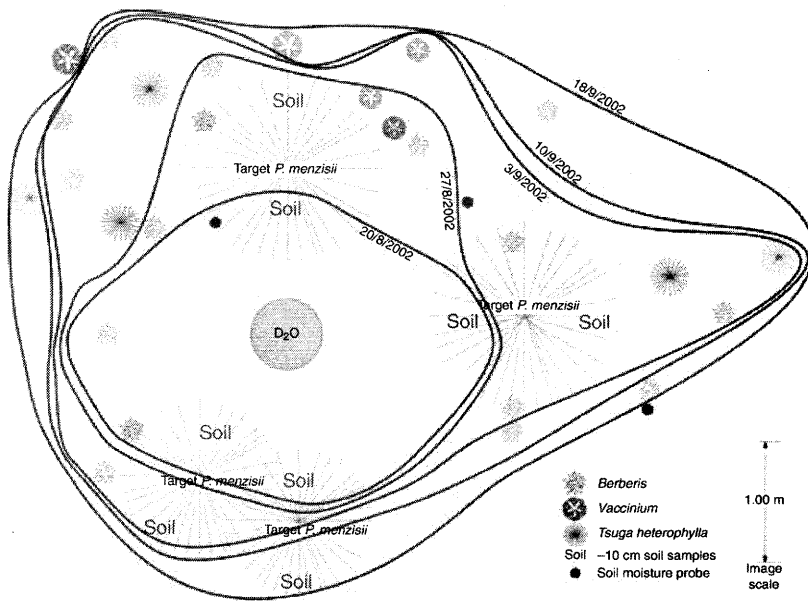| Target Douglas-fir	Maximum δD (‰)	Maximum proportion of label	Date of maximum δD	Average δD ± SD (‰)	N	Average proportion of label
1	2519	37%	9/10/2002	1557 ± 767	5	23%
2	1680	25%	9/10/2002	1068 ± 654	5	16%
3	3453	50%	9/10/2002	3297 ± 219	2	47%
4	2499	36%	9/10/2002	1909 ± 526	5	28%

Figure 5. Map showing the lateral spread of the deuterium label by hydraulic redistribution over 36 d. Each line represents the farthest extent that label was detected on a particular sampling date. Not all plant samples within a boundary were labelled (red symbols were significantly labelled, black was not), but the outer edges were determined by labelled plant or soil samples from that particular date.

on the far-side from the watering source. The highest level of label was generally found in soil samples (3–6% labelled water) surrounding the target trees both on the side near the water source and on the far side, and one Oregon grape located 2.5 m from the watering source contained 3.9% labelled water. We confined our sampling to plants within a 5 m radius of the watering site, and since we found label in these outermost plants, the labelled water was probably transported beyond our sampling boundary. However, not all plants within the sampled area were labelled, thus the distribution of labelled water was quite patchy.

At the end of the sampling period (18 September 2002), we collected samples from soil cores located near the three soil moisture probes located 1, 2 and 3 m from the watering source (note: soil moisture was only monitored at 1 and 3 m locations). Deuterated water was detected at all depths of the soil core 1 m from the watering site (Fig. 7). However, the highest concentrations were found at 10 and 50 cm with 20, 30 and 40 cm depths being substantially lower. The enrichment at 50 cm could have been due to movement of the applied deuterated water directly through the soil, but the enriched values at 10 cm for both 1 and 2 m were more likely from water hydraulically redistributed by roots and potentially mycorrhizae.
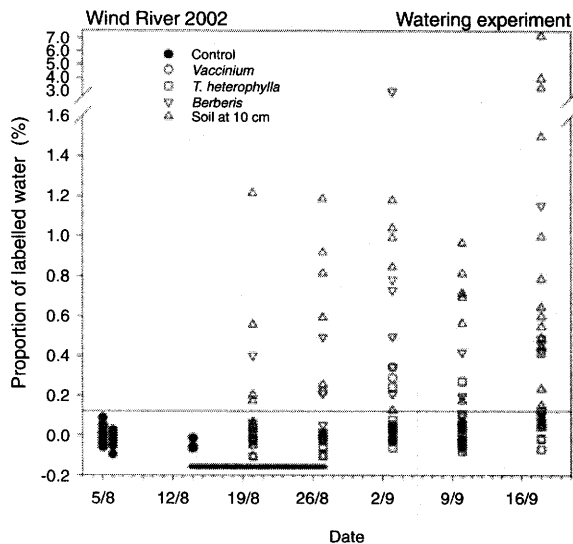

Figure 6. The proportion of deuterated water found in plant and soil samples located 1 m or more from the labelling location (See Fig. 5). The solid thick line at the bottom indicates the period when deuterated water was added to the system. All species sampled have fairly confined root systems, including the understory hemlock (Hinckley *et al.* unpublished results). The thin line at 0.11% indicates when samples were significantly different from control values.
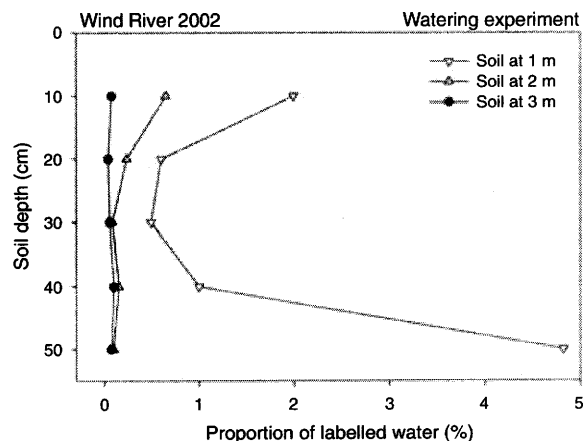

Figure 7. Profiles of deuterated water in soil samples collected at three distances from the watering site 36 d after the application of deuterated water began.
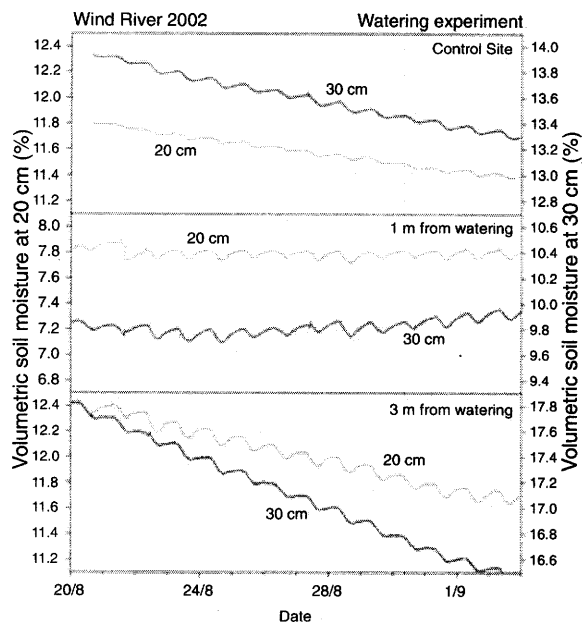
Figure 8. Diurnal changes in volumetric soil moisture measured at 20 and 30 cm depths. Soil moisture was measured at the control site, and 1 and 3 m from the location where deuterated water was added to the soil.

Volumetric soil moisture measurements made during the watering experiment indicated that hydraulic redistribution was significantly higher near the watering site relative to the control site (Figs 8 & 9. $P = 0.011$, repeated measures ANOVA). The control site and the sites near the watering all showed evidence of nightly increases of soil moisture (Fig. 8). However, the nightly increases were greater near the watering site compared to the control, and at the 1 m distance, these increases were enough to offset the daily depletion. For the 20–30 cm soil layer, the amount of water hydraulically redistributed at 1 m from the watering site was about three times the amount at the control site (0.17 ± 0.02 versus 0.05 ± 0.02 mm d^{-1} (mean $\pm$ SD), respectively), whereas the 3 m distance was about twice that of the control (0.09 ± 0.02 mm d^{-1}; Fig. 9). This nightly recharge of water influenced the amount of water utilized from the soil layers during the day (Fig. 9, lower panel). Since the amount of extractable water is influenced by θ, we standardized the daily water uptake by the amount of water stored within the soil layer. In general, daily water uptake was less than 1% of the water stored within a layer. The soils at 1 and 3 m distances from the watering site both had daily water depletion at approximately twice the rate than at the control site (0.93 ± 0.06, 0.81 ± 0.04 in comparison with $0.48 \pm 0.03\%$ of water stored). However, because of the greater nightly recharge from HR, the soils at the watering site did not dry faster than the control site. In fact the soils at 1 m from the watering site did not have a net loss of water over the monitoring period (Fig. 8).

DISCUSSION

The amount of water redistributed was relatively small, but highly significant in terms of the daily water use from a particular soil layer. The maximum rate of HR in the control plot occurred at the end of August, and was 0.17 mm d^{-1} within the 20–60 cm soil layer. The average daily soil water depletion from the same layer was only 0.4 mm d^{-1}, thus redistribution replenished approximately 50% of the water utilized daily at the end of the summer. HR fluxes were likely even higher in the 0–20 cm layer, which had much higher root density than the 20–60 cm layer (Warren *et al.* 2005), but instrument limitations prevented accurate measurements in this upper layer. Although Ψ_{soil} still declined when HR was occurring, this decline would have been much steeper without HR (Domec *et al.* 2004; Meinzer *et al.* 2004). Warren *et al.* (unpubl. data) have shown that HR is initiated along the portion of the soil moisture release curve where small changes in θ have a large impact on Ψ_{soil}. A slowing in soil drying can have a significant impact on maintaining shallow root function in the upper soil layers (Domec *et al.* 2004).

The onset of HR is tied to the development of water potential gradients within the soil–plant system. Hydraulic redistribution began in earnest in this young Douglas-fir ecosystem in late July/early August as water potentials declined to about −0.4 to −0.7 MPa in the upper soil, and soil water utilization from this layer decreased (Fig. 1). Other studies have found that HR begins when soil water potentials reach about −0.4 to −0.7 MPa (Caldwell & Richards 1989; Dawson 1993a; Millikin *et al.* 2000). In a related
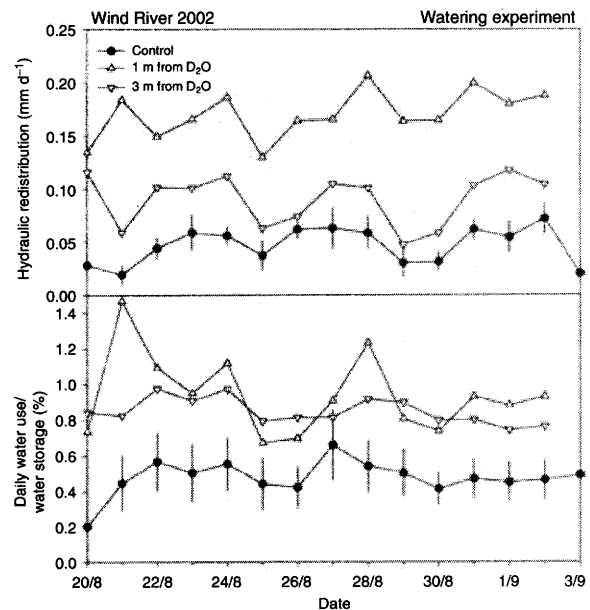

Figure 9. Daily rates of hydraulic redistribution and daily water use relative to the amount of soil water present. Values were calculated from the data presented in Fig. 8, the 20 and 30 cm layers are combined. The bars for the control symbols represent 1 standard deviation of the values from the three control probes.

study using data from the probes with maximum HR activity, Meinzer *et al.* (2004) found a threshold for HR of −0.4 MPa for this stand and five others including three Brazilian *cerrado* stands, and old-growth Douglas-fir and ponderosa pine stands. The Ψ_{soil} threshold for HR was reached approximately when upper Ψ_{soil} approached predawn Ψ_{leaf}, and thus the upper soil had become an effective competitor for water with the above-ground portion of the tree. A disequilibrium between Ψ_{soil} and predawn Ψ_{leaf} is not uncommon (Donovan, Linton & Richards 2001; Donovan, Richards & Linton 2003; Bucci *et al.* 2004) and will certainly influence HR.

If the rate of HR is regulated by competing water potential differences in the plant and soil systems, we should be able to alter the rates of HR by altering these Ψ driving forces. In this study, we increased the rate of HR by increasing the source water potential to zero (irrigation experiment), and by eliminating the competing foliage sink for water (trenching and tree removal). Increasing the source water potential increased HR from 0.05 mm d^{-1} in the 20–30 cm layer to 0.17 mm d^{-1}, over three times the rate of the control. This acceleration of HR decreased with increasing distance from the water source (0.09 mm d^{-1} at 3 m distance versus 0.17 mm d^{-1} at 1 m distance), which could reflect the greater resistance to flow due to increased path length or a dissipation of water available for HR. Increasing the amount of HR also increased the amount of water that was utilized from the soil for a given θ (Fig. 9). This finding supports the idea that HR can increase transpiration by a plant (Jackson *et al.* 2000; Mendel, Hergarten & Neugebauer 2002; Ryel *et al.* 2002).

Removing the competing foliage resulted in an even greater increase in HR with the initial values being as high as 1.3 mm d^{-1} in the 20–60 cm soil layer, but decreasing afterwards as the water potential gradient within the soil diminished with the high influx of water to the surface soils. Hultine *et al.* (2003a) also severed roots from the main tree and found reverse flow in roots no longer attached to the main tree but connected to soils with significant differences in Ψ_{soil}. They also found that in a species that exhibited night-time transpiration, reverse flow rates in roots were greater when night-time vapour pressure deficit was low. Similarly, Scholz *et al.* (2002) found that the rate of reverse flow was linearly related to $\Psi_{soil} - \Psi_{leaf}$ with the greatest reverse flow rates occurring when $\Psi_{soil} - \Psi_{leaf}$ was at its most negative values. These results suggest that the onset and maximum rate of hydraulic redistribution is regulated by interplay between the development of water potential gradients within the soil, and the nocturnal demand for water by the tree. Additionally, these results support the idea that HR is a passive process governed by resistances and water potential gradients (Mendel *et al.* 2002; Ryel *et al.* 2002).

Plants neighbouring those that can hydraulically lift water do utilize redistributed water, but quantifying the amount is difficult. In this study, we found that Oregon grape, small understorey hemlock trees, and huckleberries all took up water that was redistributed by the overstorey Douglas-fir trees (Figs 5 & 6). These species all had very

confined root systems and did not have roots directly in contact with the deuterium label. The amount of labelled water found within these plants and in the soil after 5 weeks was extremely small, generally less than 1% of their water content. These values were several orders of magnitude greater than those found by Moreira *et al.* (2003), but our irrigation design allowed for a much longer period of time for water to be redistributed and detected. Using a rare situation where natural abundance isotopes could be used to quantify the uptake of HR in understorey plants, Dawson (1993a) found that understorey plants could contain as much as 60% of water redistributed from groundwater by a nearby sugar maple. The results of our study cannot be used to quantify the amount of HR water taken up by neighbouring plants because other non-labelled trees were redistributing water as well, and our watering timeframe was limited, whereas under natural conditions, HR water would continue to be taken up through the summer.

Although understorey plants do utilize water redistributed by other plants, the benefit to understorey plants may be limited since HR doesn't begin until most of the readily available water is gone. Meinzer *et al.* (2004) found that at the water potentials where HR begins, soil water utilization has greatly declined. In this study, when HR was at its maximum, daily depletion from 20 to 60 cm had dropped from 1.5 mm per day to less than 0.4 mm, and less than 25% of the water utilized from the entire 2 m soil profile, whereas earlier the upper layer had contributed over 50%. Soil water potentials were also at a minimum, between −0.8 and −1.1 MPa. Ludwig *et al.* (2003) also felt that the understorey gained minimal benefits from HR since water potentials were significantly lower under the lifting Acacia trees they measured. Species that redistribute water are still major competitors for HR water, particularly since the water is exuded directly into their rhizosphere. However, slowing in the rate of soil drying can be a significant benefit to seedlings and other understorey plants since most of their roots are in the upper soil. HR slows water potentials from reaching critically low levels that could cause root embolism (Domec *et al.* 2004).

The use of deuterium label has helped to illustrate the extent of HR but also the patchy nature of HR within a system. Our deuterium label was found in plants up to 5 m from the watering source, which was the extent of our sampling area, thus the water could have travelled much further. However, not every plant within our sampling area was labelled. In addition, only three of the 10 roots where sapflux was monitored demonstrated reversal of flow. Warren *et al.* (unpubl. data) found that within this stand, HR varied spatially between 0.2 and 0.6 mm m^{-1} at maximum lift (late August), which reflects the heterogeneity of the soil medium and root distribution. This variance was typical of the other conifer stands they monitored in the Pacific Northwest. Ludwig *et al.* (2003) found that HR was very patchy around an African Acacia tree and concluded that root activity was spatially heterogeneous. In a tropical savanna, Moreira *et al.* (2003) found neighbouring plants as far as 2 m away could pick up trace amounts of the deute-

rium label, but generally only one or two plants surrounding the treated plant were found to contain label, again illustrating the patchy nature of HR. The occurrence of HR at a particular location will be influenced by the location of roots in addition to the water potential gradients and relative pathway resistances.

Several potential pathways exist for water to move upward or laterally in the soil: (1) liquid and vapour transport of soil water independent of roots; (2) through the mycorrhizal network (Querejeta *et al.* 2003); or (3) through plant roots. Each pathway would differ in resistance. Root resistance would be relatively minor in comparison with resistance to water flow through unsaturated soils at water potentials where HR is commonly observed (Sperry *et al.* 2002). Liquid transport between soil layers is dependent upon unsaturated soil hydraulic conductivity (K) and existence of a water potential gradient. Estimates of K for the upper soil in September were $<2 \times 10^{-7}$ cm h^{-1} based on the equations of Brooks & Corey (1964) using soil hydraulic parameters derived from soil water release curves (Warren *et al.* 2005a) and estimates of saturated soil hydraulic conductivity ($K_s = 1.08$ cm h^{-1}) based on soil texture using Campbell (1985). Variability in K_s and in the measured Ψ driving forces precludes accurate assessment of soil water flux via unsaturated liquid flow; however, estimates were <0.002 mm h^{-1}, or less than 4% of measured HR. Values of K, and thus liquid water flux is known to approach zero as the soil dries (Philip & de Vries 1957), but our measured rates of HR increased with soil drying. Vapour water flux becomes an increasing component of water movement through drying soils (Philip & de Vries 1957). The magnitude of water vapour flux is driven almost entirely by gradients in soil temperature. Since there were very small differences in temperature between soil layers at the site (Table 1), we expect vapour flux to be a minor contributor to diel patterns in soil water content assumed to be HR. Mycorrhizal resistances would also be high because of the small diameter of the hyphae, although some species produce rhizomorphs (bundles of hyphae) that have the ability to rapidly transport significant amounts of water (Duddridge, Malibari & Read 1980), and we have experiments underway to further examine the potential role of mycorrhizae in HR. These considerations, the evidence of root-mediated fluxes obtained from root sapflow, and our plant manipulations, lead us to conclude that most of the diurnal fluctuation in soil Ψ and θ, particularly in the later season, were root-mediated.

Although HR water can presumably be transported to the terminal portions of a root system and maybe further through mycorrhizae, pathway resistance may cause HR to be a more localized phenomenon. The shortest path along the least resistant route will be the pathway for hydraulically redistributed water given an equivalent water potential difference such as between surface soil and deep soil. Resistance to flow is also higher through root junctions when the water flows towards the soil rather than to the tree because water must move radially or tangentially to enter another root rather than move towards the tree (P. J.

Schulte unpublished results, Schulte & Brooks 2003), so the root resistance to HR should be greater than the root resistance to the tree. In this study, we found that early in the dry season, water was being redistributed with in the 20–60 cm layer and not coming from deeper layers until later in the dry season once the upper layer dried below −0.7 MPa (Fig. 2). In addition, only three of the 10 roots monitored for sapflow at the base of a tree showed evidence of HR. Brooks *et al.* (2002) found reversal of flow only in roots that were located on the same side as the localized watering, rather than the opposite side of the tree from the watering as expected. They hypothesized that the resistance to flow across the base of the trunk was too great for reversal of flow to be detected on the opposite side. Although in this study, we did find transport of labelled water to the opposite side of the tree and up to 5 m from the water source, we also altered the natural water potentials within the soil system. A similar ability to transport deuterated water to the opposite side of grapevines was found by Smart *et al.* (2005). Nevertheless, in a root system such as that of Douglas-fir where lateral roots send down sinkers, pathways connecting wetter deep soil and surface dry soil for HR could be very localized which would contribute to the patchy nature of HR.

In conclusion, hydraulic redistribution appeared to be an important process in the Douglas-fir ecosystem studied. Most HR occurred in the latter part of the summer as Ψ_{soil} approached predawn Ψ_{leaf} creating a competing driving force for water transport to the upper soil rather than to the leaves. The rate and magnitude of HR was strongly governed by the interplay between Ψ_{soil} gradients and the demand for water by the above-ground portion of the tree. Even though the quantity of water redistributed was small and spatially patchy, it does have profound ecological consequences particularly for the rate of root cavitation and soil drying at shallow depths where the abundance of finer roots is greatest.

ACKNOWLEDGMENTS

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